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PHENOLOGY OF THE TIMBER RATTLESNAKE *(CROTALUS HORRIDUS)* IN AN UNGLACIATED SECTION OF THE APPALACHIAN MOUNTAINS

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ABSTRACT: As part of a field study on the ecology and biology of the timber rattlesnake *(Crotalus horridus)*, seasonal activity was documented over a 17-yr period in an unglaciated section of the Appalachian Mountains centered in northwestern Virginia. Duration of hibernation averaged 6.7 months. Sporadic basking usually began from late March to mid-April with general emergence from hibernation during late April or early May. Springtime observations of adults at the dens peaked on 6 May, 3 days ahead of that for young-of-the-year and juveniles 3 yrs old or less. Mating occurred from late July to mid-September. Females spent gestation near favorably exposed rocks usually located within 500 m of over-wintering dens. Parturition occurred from August to early October. Postpartum females stayed with their litters 7-10 days, and neonates usually molted within 8-16 days after birth and then dispersed. Peak ingress occurred from late September to mid-October. Various factors, including endogenous rhythms, short-term and long-term weather trends, and photo period, control and influence the different seasonal activities.

INTRODUCTION

The timber rattlesnake, *Crotatus horridus*, is a moderately large (adults usually 85-115 cm total length), long-lived, late maturing (5-11 yr at first reproduction), viperid of the hardwood forests of eastern North America. In the Appalachian Mountains over one-half of the year is spent in hibernation. Temperatures and amount of sunlight are often below optimum even during the summer. Activity patterns are highly seasonal.

Although some phenological data can be gleaned from many studies, until now (Brown, this volume) there are no studies of seasonal activity comparable to those available for C. *viridis* in western North America (Fitch, 1949; Diller and Wallace, 1984; Duvall et al., 1985; Gannon and Secoy, 1985; Macartney, 1985); *Sistrurus catenatus* (Seigel, 1986); *Agkistrodon contortrix* (Fitch, 1960), or *Vipera berus* of Europe (Saint Girons, 1952; Duguy, 1963; Naulleau, 1966; Saint Girons and Kramer, 1963; Viitanen, 1967; Prestt, 1971; Saint Girons, 1952; Phelps, 1978; Andren, 1982; Nilson, 1980).

In this paper I examine seasonal activity patterns associated with: 1) hibernation: including ingress and emergence patterns at the overwintering dens; 2) summer dispersal, including movements of juveniles, adult males, and adult females; and 3) reproduction, including the timing of mating and parturition.

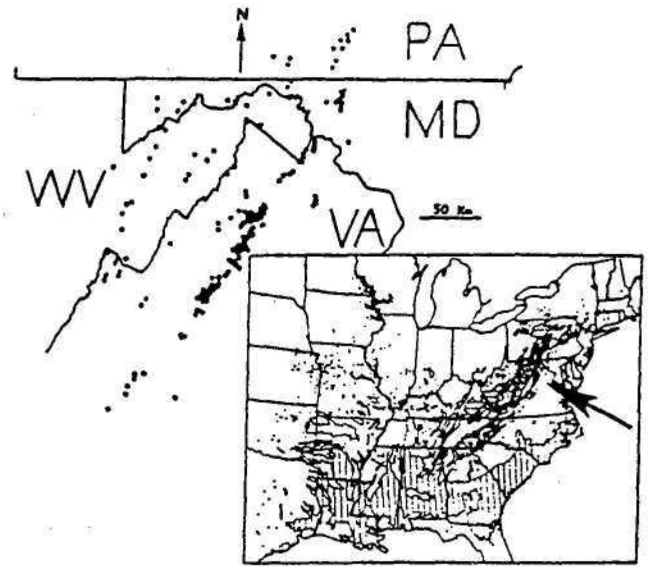

Fig. 1. Study area. Small inset map shows current range of *Crotalus horridus*. Arrow on inset map points towards study area. Solid circles indicate study sites.

METHODS

Study Area

This study was conducted in Shenandoah National Park in the Blue Ridge Mountains of northwestern Virginia (38-39° N lat., 78-79° W long.) and in nearby sections of Virginia, West Virginia, Maryland, and south-central Pennsylvania (37-40° N lat., 77-80° W long.). The study area (Fig. 1) is in the Appalachian Mountains and is located about mid-way between the northern and southern limits of the species' range within the Appalachians. The region is characterized by heavily wooded northeast-southwest trending ridges separated by agricultural valleys. Rattlesnake life centers around communal dens and birthing rookeries to which individual rattlesnakes show high fidelity (of 64 spring and fall recaptures made on snakes that were initially captured in the spring and fall, only one had switched dens - a young adult female first marked as a 3-yr old juvenile moved 2.1 km). Dens were located in ledges, talus, and scree of sandstones, quartzites, granites, gneisses, and metabasalts at elevations from 200-1200 m. Steep slopes of 3045 degrees where the winter sun strikes nearly perpendicularly were favored. Dens were of three basic types: 1) fissure or fissures in a ledge, 2) bare rock talus or scree (talus refers to an accumulation of rock below a cliff, and scree to an accumulation of rock on a slope and not associated with a cliff), and 3) talus or scree partly covered with soil. Some dens were a combination of these types and some den-colonies exhibited a diffused hibernating pattern with snakes over-wintering singly or in small groups in crevices, under slabs, or in small patches of rock spread out over a hectare or more. Within the study area I confirmed the location of hibernating crevices at 115 of 153 den-colonies where rattlesnakes were found in the spring or fall. Of these 153 sites, one faced due north, two faced due east, 10 faced northwest, and the remaining 140 faced in southerly or westerly directions from southeast to due west. Rattlesnakes were found during,

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1992. Pages 259-277 In Campbell, J.A. and E.D. Brodie Jr. **Biology of the Pitvipers.** Selva, Tyler, Texas.

the summer months at an additional 85 probable den sites which I did not check in the spring or fall. Of the 115 confirmed hibernacula, 47 were located in heavily shaded locations. All, however, were located within 500 m of well exposed basking areas. Den spacing averaged 1.68 km (range, 0.25-4.5) for 99 Shenandoah (Virginia) dens and 0.95 km (0.35-32) for 19 Catoctin (Maryland) dens. Total populations at the 10 largest dens in the area were estimated by mark-recapture to be comprised of 120-200 snakes each. Populations of most dens were believed to range from 30-60 snakes. Dens were sometimes shared with lesser numbers of the northern copperhead *(Agkistrodon contortrix mokasen)* and several species of non-venomous snakes, with the black rat snake *(Elaphe obsolete obsoleta)* being the most frequent of these.

The climate in this region is temperate with precipitation fairly evenly distributed through the year but droughts do occur occasionally. Mean daily maximum and minimum temperatures for Shenandoah National Park Headquarters at Luray, Virginia, at 365 m, are *292* and 14.9° C, respectively, for July and 5.8 and -7.0° C, respectively, for January. Corresponding temperatures for Big Meadows, Virginia, near the center of Shenandoah National Park, at 1077 m, are 23.9 and 14.4° C for July, respectively, and 1.9 and -7.7° C, respectively, for January (Table 1). Annual precipitation averages 104.4 cm for Luray and 129.5 cm for Big Meadows. The duration of the frost-free season is 155-165 days for these two stations and ranges from 140 to 180 days throughout the study area (USDA, 1941).

A continental high is the major influence on the weather from October to May. The ground is usually frozen from late December to early March, and snow cover is often present. The continental high begins weakening in May. From early June until early September the major influence on the weather is the Bermuda high which brings warm moist Gulf air with frequent thunder storms.

The thermal gradient reverses in October as soil temperatures near the surface fall below 10-12° C. The middle layers (around 45 cm) are usually the warmest (around 15° C) and are interposed between cooler layers. By January and February temperatures at depths of 30-50 cm usually range from 1-6° C. The 0° C isotherm usually reaches 45 cm (its deepest level) in February during most years. Base temperature (deep ground temperatures below 3 m and large springs and caverns) correlate closely with mean annual temperature which in the study area is about 10-12° C. A partial reversal of the thermal gradient occurs in March when the surface layers exceed 8° C and are warmer than the middle layers but still usually cooler than the base temperature of 10-12° C. By late March or early April, surface temperatures warm to 11° C or more and 80-100 cm levels reach 5-7° C. In late April or early May, the 10-11° C isotherm penetrates to about 45 cm. Soils become nearly isothermal in May at temperatures of 10-12° C (Table 1).

Study Procedures

Sampling was non-destructive. Snakes found dead-on-the-road or brought to me dead were dissected. Field work was conducted mainly from April 1973 to October 1989 with additional observations during 1956-1971 and 1990-1991. The most intensive sampling was during spring emergence in late April to mid-May and again at birthing time in late August and September when field trips averaged one every second day, with the weather usually determining the schedule. Snakes were sexed, measured (snout-base of rattle), and marked uniquely with a number in indelible ink on the basal segment of the rattle. Sampling was usually limited to days with temperatures of 15-30° C. Partly cloudy days were favored for sampling. One den was visited 36 times in 1974 but after noting increasing difficulty finding snakes on successive visits, I usually limited the number of visits per den site to 1-4 per year. In order to minimize my effect on the behavior of the snakes, most dens discovered after 1985 were reserved for phenological observations only and no snakes were captured at these dens. The number of field days during the period 1973-1990 averaged 59 (range, 32-112) per year, and the number in my primary study area averaged 45 (range, 8-82) per year. Field days in the study region totaled 981 with monthly totals as follows: March (5), April (87), May (214). June (129), July (151), August (159), September (139), October (92), November (10). A total of 5926 rattlesnakes, including 1372 neonates, was examined in the field during the study. To avoid unnecessary biases, samples from the dens; the roads; and those found incidentally in the woods away from the dens, were examined separately.

In order to obtain relevant ecological data, I adapted a phenological calendar based on principals used by agriculturalists (Hopkins, 1938). The system is based on the movement of the sun's azimuth 15' a day (about 24 km) and on the adiabatic lapse rate and its influence on the upward movement of the vegetation lines an average of 40 (10-100) m per day in the spring and 50 m per day in the fall (Martin, unpubl. data).

I examined the soil temperature and blooming records from the West Virginia University experiment farm located at about 150 m elevation in Jefferson County, West Virginia, slightly north of the geographic center of my study area. Soil temperatures were recorded daily from 1978-1989 at a depth of 10 cm and sporadically at 30 cm. I also examined soil temperature records from the Fruit Research Laboratory located at Biglerville, Adams County, Pennsylvania, elevation 200 m near the north end of the study area. Weekly high and low readings were recorded for 1984-1989 at depths of 20 and 45 cm. The United States Department of Agriculture experiment farm located near the geographic center of the study area in Frederick County, Virginia, 230 m, provided blooming records for apples and peaches. The National Park Service provided temperature and precipitation records for Luray and Big Meadows in Shenandoah National Park, Virginia, and for Catoctin Mountain Park, in Maryland.

RESULTS

Onset of Hibernation

In autumn, most rattlesnakes were observed from 28 September to 18 October, with observations peaking on 6 October (Fig. 2). For nine of 13 years, the dates for the first snakes seen in the den crevices were from 26 September to 2 October (Table 2). During 1983 and 1984, in spite of my searching during favorable weather in that period, I found no snakes in the dens until 8 and 4 October, respectively. First snakes were seen in the dens in 1974 on 23 September, and in 1986 I found two postmolt neonates in den crevices on 7 September at a den at near 775 m elevation. By 18 September 1986 rattlesnakes were returning to dens located around 400 m elevation.

Temperatures at Ingress

Autumn temperatures varied widely from year to year, with lows during the week preceding first arrivals ranging from -2 to 8° C, yet ingress usually began at about the same time regardless of the weather. The high degree of conformity of dates of ingress between years suggests that a biological clock is involved. During 1983 and 1984, when the snakes were late returning to the dens, emergence had been delayed by cool and wet spring weather. In 1974, when the snakes returned a little earlier than normal to the dens, a hard freeze with lows of -2° C occurred on 23 September, about three weeks earlier than the average date for a hard frost. The fall of 1986 was the only time that ingress occurred significantly earlier than average. An early emergence that year was followed by a hot dry summer and then the first cold fronts with scattered light frost began in late August. With the exception of photoperiod, all indicators of fall were present much before normal.

The mean date of ingress approximately corresponded to the mean date that the temperature mean fell below 11° C. This date also corresponded closely with the mean date of the first killing frost (USDA, 1941).

During most years, most of the snakes had arrived at the

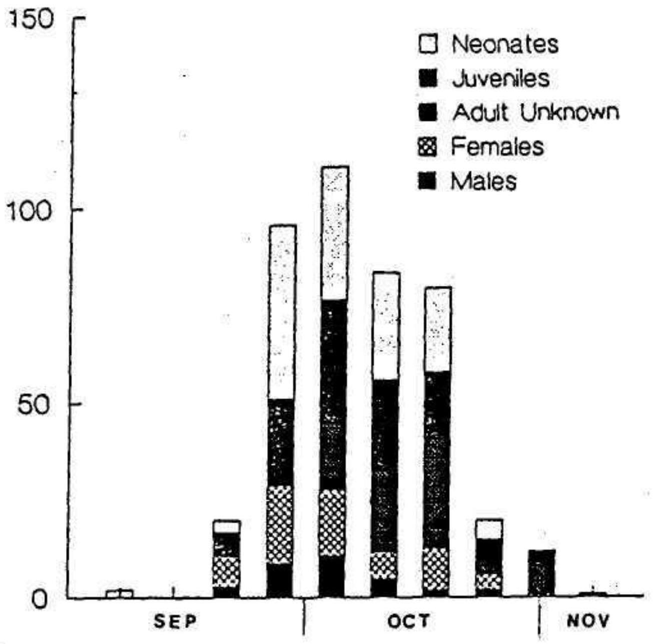

Fig. 2. Number (n = 426) of *Crotalus horridus* seen during the fall (September-November) in overwintering crevices, within 10 m of overwintering crevices, or within the area encompassed by overwintering crevices in multi-crevice dens, for all years combined. Sample was broken down by sex and age-class. Snakes that showed less than eight marks were considered juveniles. Females and neonates seen at birthing rookeries are not included.

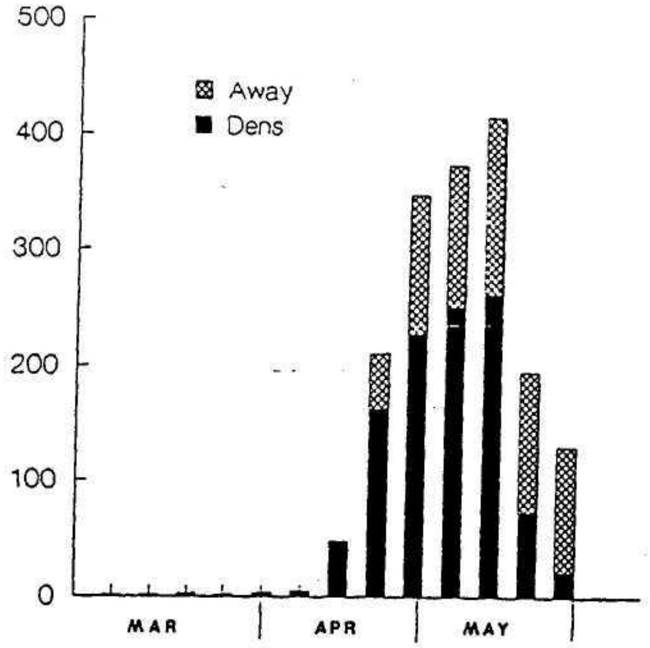

Fig. 3. Number (n = 1736) of *Crotalus horridus* seen at the dens and away from the dens in the spring (March-May) for all years combined. Snakes in overwintering crevices, within 10 m of overwintering crevices, or within the area encompassed by overwintering crevices in multi-crevice dens, were considered to be at the den.

dens by 16 October and any snakes seen after that date were usually in or next to den crevices. However, in 1983 when the snakes were late coming into the dens, I found five rattlesnakes at the edge of the woods adjacent to a den on 28 October. The latest date on which I found a rattlesnake on a road was 20 October.

Individual snakes apparently do not usually stay on the surface for long after arrival at the dens. With the exception of postpartum females and premolt neonates, only once did I find the same snake on follow-up visits in the fall after more than four days had elapsed. The latest date on which I have found a rattlesnake was 5 November, and nine of 13 snakes seen in November were inside den crevices. I received reports of rattlesnakes, usually solitary individuals, found by deer or upland game hunters during mild weather in the late fall and early winter, but my efforts to find rattlesnakes at the dens were unsuccessful from mid-November to early March. I speculate that most of the snakes reported during this period were probably solitary hibernators using shallow shelters from which they were relatively easily roused by the weak winter sun.

The most productive fall days occurred during partly cloudy weather with high temperatures of 20-27° C. The best fall days were slightly less productive than the best spring days and considerably less numerous (Figs. 2 and 3). On the most productive fall day, 35 snakes (including six young-of-the-year were seen. Snakes were active at a lower temperature in the fall than during other seasons. On 13 October 1974, I found three dead rattlesnakes on the road with local highs of only 16° C and the weather mostly cloudy. Snakes were occasionally found basking at dens with temperatures as low as 11° C and crossing roads at 12° C.

Table 1. Air and soil temperatures in degrees C for the study area. Mean monthly air temperatures are listed for Luray, Page County, Virginia at 365 m. and for Big Meadows in Shenandoah National Park, Virginia, at 1077 m for the period 1973-1989. Mean soil temperatures at 45 cm depth are listed for the Biglerville Fruit Station, In Adams County, Pennsylvania at 200 m for the period 1984-1989.

Month	Luray		Big Meadows		Biglerville
	High	Low	High	Low	Avg
1	5.8	-7.0	1.7	-7.8	1.4
2	6.3	-6.6	1.9	-7.8	0.8
3	12.4	-1.6	6.7	-1.6	32
4	18.3	3.0	12.9	3.0	7.4
5	23.5	8.0	17.8	8.0	12.0
6	27.7	13.0	22.4	13.0	16.8
7	29.2	14.9	23.9	14.9	20.7
8	28.7	14.2	23.1	142	21.1
9	24.8	10.4	202	10.4	183
10	20.0	4.3	13.9	4.3	13.0
11	13.3	-0.3	8.3	-0.3	8.4
12	7.6	-4.1	42	-4.1	4.0

Table 2. Dates of emergence and ingress for *Crotalus horridus*. The median date (mo/day) is listed for snakes seen at the dens. Dates of first and last snakes seen in dens are shown in parentheses. Peak emergence is estimated by the numbers and location of snakes seen. Full bloom dates for apple trees were obtained from the University of West Virginia experimental fruit station, in Jefferson County, West Virginia. Temperature deviation from the mean for the 1973-1990 period is shown in degrees C for Luray, Virginia. Dashes indicate that I was not in the study area during the appropriate time. In 1976 general emergence was well-advanced by the time I arrived at the study area and in 1978 and 1979 I was not in the study area for the first part of emergence.

Yr	Emergence med	(range)	peak	Apple bloom	T deviation Feb-April	Ingress med	(range)
–							
73	5/5	(4/30-6/2)	5/1	4/25	+0.2	10/12	(1002-15)
74	5/3	(3/8-5/25)	4/29	4/27	+0.3	10/6	(9/23-11/4)
75	5/11	(5/7-21)	5/14	5/8	-12	10/11	(10/1-11/5)
76	4/24	(4/23-5/10)	4/18	4/15	+2.7	10/13	(10/13-16)
77	5/2	(4/16-5/15)	4/22	4/16	+1.2	10/1	(9/30-10/9)
78	5/18	(5/10-22)	5/10	5/4	-2.6	–	
79	5/9	(5/6-22)	5/6	4/30	-1.9	–	
80	5/4	(4/18-5/12)	5/4	5/4	-1.9	10/8	(9/29-10/9)
81	5/6	(3/31-5/13)	4/30	4/24	+0.6	10/17	(10/5-21)
82	5/9	(4/16-5/15)	5/5	5/2	-0.4	10/2	(10/2-11/2)
83	5/6	(4/26-5/25)	5/6	5/3	+0.1	10/28	(10/8-28)
84	5/12	(4/26-5/21)	5/12	5/6	-0.3	10/10	(10/4-18)
85	4/27	(4/5-5/7)	4/20	4/22	+1.4	10/1	(10/1-18)
86	4/29	(3/29-5/16)	4/29	4/25	+0.5	9/27	(9/7-10/9)
87	5/1	(3/30-5/12)	5/2	4/28	-0.4	10/2	(9/26-10/18)
88	5/7	(4/5-5/29)	5/7	5/3	+03	10/9	(9/30-10/17)
89	4/26	(3/29-5/22)	4/30	4/26	-0.4	10/16	(9/29-10/27)
90	4/24	(3/14-6/2)	4/25	4/25	+23	10/6	(9/20-11/2)
*	5/4	(4/14-5/19)	5/2	4/28		10/9	(9/30-10/21)
range		(3/8-6/2)					(9/7-11/5)

Only in 1976 did I have any indication that numbers of snakes may have failed to arrive at the dens. Temperatures during the normal ingress period were considerably below normal and continued below normal until mid-winter. On the last mild day, 16 October, with a high temperature of 12° C, I found a rattlesnake on a road *12* km from a den. Later that winter, I got reports of three rattlesnakes found from 1.54 km away from dens during the months of November, December, and February. Several times during the study, ingress was interrupted by a week or more of cold or even snowy weather in early October, but mild weather resumed in mid-to-late October and the snakes resumed the migration.

When the temperature range remained above normal (lows in excess of 8° C and highs in excess of 20° C), snakes were sometimes found in the wooded areas adjacent to the den where they apparently foraged before coming into the den. On 13, 19, 22, 28 and 29 September, and 1. 3, and 9 October, I found rattlesnakes in wooded areas adjacent to dens, where they were coiled In characteristic ambush positions. On the latter date two individuals were seen moving into the woods from the den.

Ontogenetic and Sexual Differences in Time of Arrival at the Dens.

The time of arrival at the dens and the time of going under ground is not correlated with sex or age with one exception (Fig. 2). Premolt neonates stay out at birthing rookeries or dens until they have molted or, in a few cases, are forced underground by cold before molting. During 1974, 1981, 198[illegible]-1984, and 1989 birthing was delayed past the normal time by cool wet weather in the spring or summer. Litters of premolt neonates were found basking on 10, 14, 16, 17, 21, and 26 October during those years.

Differences in Timing of Ingress due to Elevation

I compared fall records of snakes at the lower dens of 200400 m with those at higher dens of 800-1200 m. Records for 39 snakes at the lower dens peaked on 17 October and ranged from 2-28 October. Records for 73 snakes at the higher dens peaked on 28 September and ranged from 19 September to 11 October.

Depth of Hibernation

The depth at which rattlesnakes hibernate is poorly known. On 15 April 1961, I excavated an apparent solitarily hibernating adult female from a depth of about 25 cm on a south slope. The late Roy Sullivan (pers. comm.) stated that at what is now Brown Mountain Overlook, the work crew of which he was a member, dug up a rattlesnake den during construction of Skyline Drive, the motorway through Shenandoah National Park. The den was said to have been uncovered on a west slope about 6 m into the hillside in a mixture of shale, sandstone, and earth, and to have contained about 20 adult rattlesnakes.

In four horizontal crevice dens that apparently lead to overwintering chambers it is possible to peer about 1-2 m. [illegible] snakes were ever seen by me on visits from mid-November to early March at those or other dens.

The frost line (0° C isotherm) usually penetrates to about 45 cm (USDA, 1941) depth on level ground, but during the extremely cold winter of 1976-77 the frost line may have reached to about 80 cm (various unofficial sources). The hibernating chamber in a communal-ancestral den should be below the maximum penetration of the frost line at a depth of at least 80-120 cm on level ground. Frost line depth varies according to aspect, slope, and soil characteristics.

The minimum temperature that this snake can tolerate has not been established. A captive that was accidentally subjected to several hours of -2.2° C subsequently thrived for over a year at which time he was released.

Length of Hibernation

On average, hibernation lasted 204 days (Table 2) from 10 October to 1 May. For a few individuals, the time in the dens may have been as little as 170 days (28 October to 16 April) or as long as 268 days (7 September to 2 June).

First Emergence

Some temporary emergence usually occurred 1-8 weeks before termination of hibernation and general emergence (Table 2). The number of snakes seen at a den during these periods in March and early April ranged from one to three. During 12 of 16 years, first snakes were seen from 29 March to 15 April but in 1983 and 1984, I found no snakes until 26 April. Only in 1974 and 1990 did I find snakes during the first half of March.

Temperatures at First Emergence

High temperatures recorded on days of temporary emergence ranged from 20 to 28°C and lows from 1 to 14°C. First emergence was never observed on the first day that temperatures were within this range, but occurred after two to seven days of mild mostly sunny weather. On days preceeding general emergence, I observed basking between 1200-1600 hr. The few snakes that came out early in the year, apparently usually returned to hibernating crevices in the late afternoon. During most years, first emergence was separated from general emergence by fairly long periods of inclement weather, but in 1977 first emergence and general emergence were apparently continuous and graded from one into the other due to uninterrupted mild weather.

General Emergence

The earliest date that I have found snakes moving away from the dens were 9 and 16 April. The median date for all snakes found at the dens in the spring was 6 May (Fig. 3) and the mean of the years was 4 May (24 April-18 May) (Table 2). I subjectively estimated the date of peak general emergence (based on the time when I believe 50% of the population was on the surface and had left den crevices) for each year based on the number of snakes I saw at and around dens and basking areas. The mean of the years was 2 May (18 April to 14 May for different years).

Temperatures at General Emergence

On days of general emergence, low temperatures ranged from 0-15° C and highs from 20-30° C. The wide range of weather conditions at general emergence suggests that ambient air temperature plays a minor role in triggering emergence. The mean date of emergence corresponds with the mean date that the 12° C isotherm is reached. When the 3-month average temperatures from February to April are examined, a strong relationship is apparent (Table 2). However, several inconsistencies are noted in this table. Emergence during the years of 1983, 1984, and 1988 was later than we would have predicted from the 3-month temperatures. This aberration is explained by weather conditions. During those years, mostly cool (below 15° C) cloudy weather occurred in early May just at the time when general emergence was beginning or about to begin.

Duration of General Emergence

The duration of emergence (first and last snakes out) at mid-elevation dens (400-800 m) ranged from four to 40 days (Table 2). When day and night temperatures were high (highs of 27-30° C and lows of 11-14° C) as in 1985 and 1990, most snakes emerged and dispersed in about four days from 18 to 20 April and 23 to 26 April, respectively. When day and night temperatures were low (highs of 6-25° C and lows of 0-9° C) and cloud cover high, emergence was much prolonged lasting from 19 April to 10 May at most mid-elevation dens in 1987. Typically the period lasted about 10-14 days at mid-elevations with snakes on the surface on about half of the days whenever there was some sun and temperatures exceeded 15° C. At the highest elevations in 1990 general emergence apparently lasted from late April to extreme early June in contrast to four to five days at low to middle elevations.

The duration of emergence depends not only on the weather but on den characteristics. Snakes tended to stay longer at dens that were well-exposed to the sun, especially if there were no other good basking habitats nearby.

Most emergence takes place between 0900-1800 hr. The onset of emergence depends on the weather and on the orientation of the dens. Snakes usually did not emerge until the sun had reached the den entrance unless temperatures were well above average. During dear weather the rocks may get too hot in the early afternoon arid the snakes often exhibited a bimodal emergence pattern with the major emergence occurring in the morning and a secondary emergence late in the day. During unseasonably hot weather the snakes left the dens at or after sundown.

Difference in Emergence Due to Elevation

The bulk of my observations were at middle elevations (400-800 m) where 87 of 152 dens were located. I compared emergence data for the lower dens (200-400 m) with that for the higher dens (800-1200 m). For 259 snakes found at the lower dens for the March to May period, the peak occurred on 1 May. Earliest snakes were found on 16 March. Excluding gravid females, the latest any snakes were found in these dens was 20 May. Eliminating the 33 gravid females that were later than that date, moves the peak of observations to 30 April. Observations on 208 snakes found at the high dens ranged from 2 May to 2 June and peaked on 14 May.

Differences in Timing of Emergence Due to Den Orientation

General emergence usually occurred first at the most open, south-southwest facing dens. Emergence from east and northwest facing dens of similar elevation ranged from one to seven days behind the more southerly facing dens, depending on temperatures. General emergence at a north-facing den was delayed 2-14 days past that of other dens of similar elevation that faced south or southwest.

One of the dens that experiences an extremely early emergence faces east but is only 275 m in elevation and snakes den in relatively shallow shelters under slabs. A southwest-facing den at 800 m elevation located among large boulders has a consistently later emergence than others of similar exposure and elevation; the late emergence is probably attributable to a later warming due to the thickness of the large boulders under which the overwintering crevices are located.

Differences in Timing of Emergence Due to Sex and Breeding Condition

No difference in timing of emergence between the sexes was noted (Fig. 4). After mid-May the proportion of females increased due mainly to gravid females moving to birthing rookeries. Some individuals, especially adult males and postpartum females left the den area on the first day of emergence and apparently moved into the woods towards summer range. On 28 April 1991, an adult male was found 1.3 km from a den. On 8 May 1975 during emergence time in a year with a late spring (Table 2), an adult male was found crossing a road 500 m from the den. Temperature range that day was 4-21° C. On 9 May 1988 a postpartum female was found 12 km from the den.

Many snakes, especially gravid females and non-postpartum females, made considerable use of exposed shelter rocks that were used for basking in the mornings and sometimes late afternoons. Especially favored were those slabs located on steep southerly slopes exposed to the perpendicular rays of the sun. These rocks provide shelter from the hot noon sun and from cooling rains, and retain heat during the night, protecting the snakes from the occasional frosts, and probably allowing them to maintain a higher body temperature than they would otherwise be able to maintain. Although some of these shelter rocks are in open and exposed places, some are in partially shaded areas but because trees are just beginning to leaf out at emergence time, the sun is barely prevented from shining through. Within about two weeks, the trees are completely leafed out and some of these shelter rocks are in the shade. Shelter rocks that were most heavily used in the spring were those located at the dens or within 100 m of the dens; those located up to 350 m distant were also frequently used. The leafing of trees may also increase humidity and night-time temperatures thus providing a warm blanket of air. In late April 1985 and 1990, the weather was so hot and dry that most of the snakes either moved to summer range or to cooler northerly slopes immediately upon emergence.

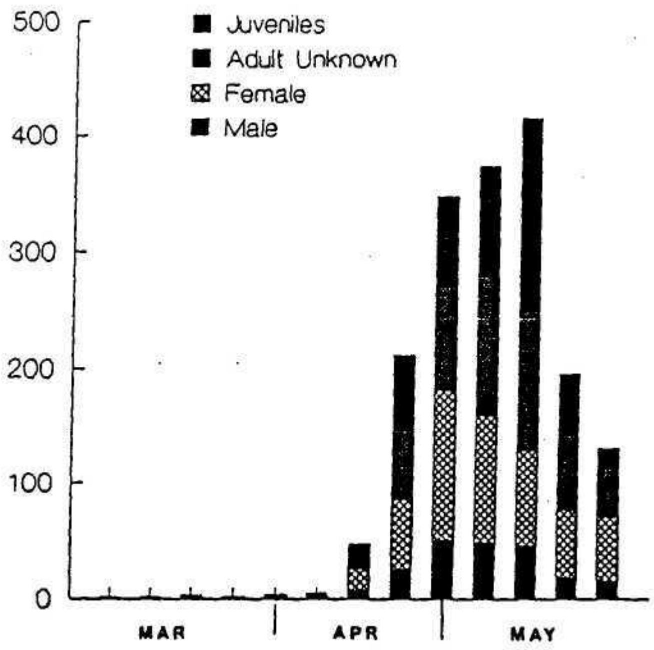

Fig. 4. Number (n = 1736) of *Crotalus horridus* seen in the spring (March-May broken down by sex and age-class.

Duration of Spring Basking Period

The number of snakes seen at basking rocks away from the immediate den area was about half the number seen at the dens through mid-May (Fig. 3). Sightings at basking areas peaked in mid-May about a week behind sightings at the dens;, and after mid-May exceeded those at the dens.

Denning Habits of Young-of-the-year

A substantial but unknown proportion of young-of-the-year do not spend their first winter in communal hibernacula. My observations suggest that only about 30% are overwintering at communal dens. Of 1566 snakes found in the spring, only 52 were young-of-the-year. In contrast, of 333 found at the dens in the fall, 140 were young-of-the-year. One might argue that because of their small size they are simply overlooked in the spring. Because of my experience in the fall I do not believe this to be entirely the case. Young-of-the-year are quite conspicuous in the fall and although it may be that through experience they learn to be more secretive, they may also disperse considerably. Several hibernacula are known to be used largely or entirely by smaller rattlesnakes. These dens probably have crevices that are too narrow to accommodate the larger snakes and, in fact, the crevices in which small snakes have been seen are often narrow. Many young-of-the-year may simply be finding individual shallow shelters, where mortality is likely to be high due to freezing. Once on 17 October I found four young-of-the-year preparing to hibernate about 30 m from a rookery and about 100 m distant from a communal den. They were seen again four days later, but in spite of visits the following spring and several subsequent springs and falls, I never saw snakes at that exact location again. In western North Carolina, I found a young-of-the-year on 2 May at a birthing rookery where the little snake had apparently over-wintered. Frost lines at that latitude are considerably shallower than in northwestern Virginia, due to the milder winters (USDA, 1941).

Emergence of juveniles under four years of age averaged about three days behind that of the adults (Fig. 4). However, some juveniles emerged with the earliest emerging adults.

Spring Migration

The period from mid-May to early June is transitional from spring to summer. The continental high weakens and warm moist Gulf air begins to move into the area sporadically at first until by the second week of June when dry continental air masses are only occasional. Weather is extremely variable, with rare light frosts and lows averaging 8-12° C.

The beginning of the spring migration and foraging period begins with the onset of the first warm, humid, summer-like evenings. Although during most years a few snakes left the den area in late April for foraging, (accomplished by coiling in ambush positions apparently along prey scent trails), it was usually mid-May before the den and spring basking areas were deserted. On 28 April 1985, a recently fed postpartum female was found 300 m from the den where she had been marked the previous year. Following the first or second warm night of the year, I sometimes found snakes that had taken up ambush positions in the wooded areas adjacent to the dens and spring basking areas, but as the season advanced the snakes spread progressively further and became increasingly difficult to find.

Although some snakes left the vicinity of the dens in late April of 1977, only in 1976, 1985, and 1990 did most of the population leave the dens and move into the woods during late April (Table 2). High temperatures during 12-14 April of 1977 were of record levels, but these temperatures came before most of the snakes had emerged. The high temperatures hastened emergence, but by then temperatures had returned to more normal levels.

Early Summer Peak

An activity peak involving nearly all snakes with the exception of gravid females and premolt snakes, usually occurred about the second week of June but sometimes was in late May or not until early July. This activity usually occurred during the first period of settled summer weather with lows exceeding 13° C and highs of 22-27° C or higher. The duration of this activity was usually about 1 week. The highest number of snakes observed dead on the road that contained food was in May and June. Snakes that had recently fed were mostly sedentary and not often found on roads. Of 112 road-killed snakes, only nine contained food in their stomachs. Two of these were found during May, four in June, one in July, and two in August

Summer Range

The bulk of the rattlesnake population moves away from the dens into wooded or brushy areas for foraging. Exposed rocks, either near or distant from the dens are much used by snakes of various age-classes and both sexes that are in a premolt condition. The rock retaining walls along Skyline Drive and other mountain roads are commonly used. The average distance to the nearest den for 126 snakes found alive or dead on the roads was 1.2 km ± 0.6 (range, 0.3-2.8 km). The mean distance to the nearest den for adult males was 1.28 km (range, 0.4-2.8 km; n = 48) for adult females 1.08 km (range, 0.4-2.6 km; n = 30), and for juveniles up to 75 cm total length 1.07 km (range, 0.4-2.5 km n = 48). Only four of these were marked snakes whose den was positively known. An additional 18 snakes found in areas where I was not familiar with the local distribution of dens, are not included.

The monthly distribution for the 144 snakes was: May (6); June (25), July (41), August (41), September (20), October (11). During June to August an additional 78 rattlesnakes were encountered away from the dens and rookery areas. The mean distance to the nearest den was 1.1 km (range, 0.3-2.1 km) for 28 adult males and 0.9 km (range, 0.15-2.1 km) for 27 adult females. For 16 juveniles the mean distance to the nearest den was 1.2 km (range, 0.45-1.9 km). For the remaining seven snakes, my knowledge of the location of local dens was poor. Six rattlesnakes that were reported by park service personnel and not examined by me were found at distances of 5.5-6 km from the nearest den. In most cases in which rattlesnakes were found away from the dens, there was either continuous wooded country or a wooded corridor leading to the den.

Seasonal Movement and Activity of Adult Males

The proportion of males in the adult spring sample does not change significantly from 30% until after mid-May (Fig. 4) when the proportion drops to below 25%. The numbers of adult males found in the vicinity of the dens were: April (59), May (158), June (57), July (58), August (88), September (45), October (30).

A recapture rate of 13.2% for adult males versus 16.6% for adult females suggests males are more difficult to recapture and are under-represented by about 25.8% (205/814 adults marked were males and 27/128 adults recaptured were males). This may be because males spend much less time around the open sunny exposures during the summer than do females. Thus males may actually make up about 30-35% of the adult population just as they make up about 30% of the spring catch and 34% of the fall catch (Figs. 2 and 4). The number of adult males found around the dens, began to increase in late July, peaked in August, and fell off sharply after mid-September. Adult males are among the first to leave the dens. Only a limited amount of basking is done during the post-emergence period. They forage actively until late July when the mating season commences and the males begin long-distance movements apparently in search of receptive females. A peak of activity was noted in late July and early August for adult males. It is not uncommon however, to find adult males in the vicinity of birthing rookeries during any month but these observations peak in August and early September. In the vicinity of some dens there are areas that are much used by males and non-gravid females. About 150 m from one den and 50 m from a birthing rookery is one such area where it was common to find from one to three adults, but never a gravid female. The area consisted of a small, partly shaded, boulder field on level ground. Obviously the opportunities for thermoregulating are inferior to the nearby rookery. Twice there, in late July and August, I found marked males from a different den 400 m distant.

Male-female pairings of rattlesnakes peaked in early August. Aggregations that included at least an adult male and adult female, totaled 41; 18 pairings occurred during August, 13 in July, and 10 in September (5 July-15 September). Three of these aggregations included two pairs. Mating was observed 21 August 1976, 5 September 1978, and 13 September 1979. Although most of the pairs were found at or within 350 m of dens or birthing rookeries where my activities were concentrated, undoubtedly much of the mating activity occurs on summer range away from dens. Male combat (ritualized fighting) was observed on 31 July 1976 at a distance of 0.6 km from a den at a Park Service Development and 25 August 1977 at a den-rookery area. Males feed little during the mating season. Captive adult males usually fasted or fed sparingly during late July to early September. Pairings waned around mid-September and males moved off into wooded areas and resumed foraging.

Seasonal Movements of Non-gravid Females

Females reproduced at 2-5 yr intervals (Martin, unpubl. recapture data). Foraging usually begins mid-May and continues until late September. In late July or August, vitellogenic females often begin to appear at or near birthing rookeries. They spend an increased amount of time basking, probably in order to maintain an optimum body temperature and speed yolk deposition. They do not, however spend all their time at these exposed locations but continue to forage in the vicinity. On 27 August 1987 following a brief shower, I observed a vitellogenic female moving through the grass away from a birthing rookery about 10 m distant. About 5 m behind this female was a second vitellogenic female, apparently following her scent trail. Non-gravid females have also been found on roads considerable distances from dens during this season. One found on 12 August 1975 was 2.6 km from the nearest den. Non-gravid females are rarely seen at birthing rookeries in late September when nearly the entire population of rattlesnakes is engaged in the early fall foraging phase of activity.

Seasonal Movement of Gravid Females

An increased tendency to bask, either at birthing rookeries or at the spring shelters, was noted with gravid females. Along with the rest of the population, they usually became difficult to find around mid-May when they moved into the wooded areas near the dens. Foraging gravid females were found 12, 22 and 30 May and 12 and 22 June. These individuals were either coiled in an ambush position or appeared to be searching for prey trails. Gravid females found on 18 May and 25 May contained large food items. These females usually move to the birthing rookeries in late May or June, probably after ovulating and becoming pregnant from the previous summer's mating. The earliest aggregation of gravid females I have found was on 18 May 1987 when five of them were found at a birthing rookery and three more nearby. Some pregnant females, however, apparently do not reach the birthing rookeries until late summer. I found a road-killed female on 1 July, 1.3 km from a den. Tom Atkinson (pers. comm.) found a pregnant female on a road 0.8 km from a den on 17 August 1982. She gave birth a I month later in captivity.

Aggregations of gravid females totalling 20, 15, 13, 12, 11, 11, and several of nine and 10 were found from late May to September. They are gregarious and often lay in contact with each other even when there are several rookery rocks in close proximity from which to choose.

Pregnant females normally do not feed during gestation, which extends for a three- and sometimes four-month period, but one found on 15 July contained a large food item and another captured 4 July accepted a dead chipmunk on 11 July. David Storment (pers. comm.) reports that an Illinois captive fed on 9 July and birthed on 1 September.

Gestating and Birthing Rookeries

Certain favorably exposed rocks are used as gestating and birthing sites. During this study, litters were found at 65 sites. For all but 10 of these litters, the location of the parental female hibernaculum was known. For 14 of these sites, birthing occurred at the den or within the area encompassed by the hibernating crevices. For 42 locations in which birthing occurred away from the dens, the mean distance was 164 m (range, 25-1250 m). For two of the sites in which the birthing rookeries were located at the over-wintering dens, there also existed alternate birthing rookeries 150-300 m distant. I was able to confirm the repeated use of 48 of the birthing sites. The greatest distance from the overwintering den for birthing sites definitely used more than once was 1.1 km. A road-killed, near-term pregnant female found on 9 September 1979 was *13* km from a den and had apparently used a rock retaining wall as a rookery.

The most common type of birthing rookery was a rock slab located on a ledge, a grassy slope or a flat; about 40% (26) of rookeries fall into this category. Rookeries located in talus, scree, or boulder fields made up 29.7% (19) and 28.1% (18) of the total consisted of a crevice located in a ledge. One litter was located in a rockpile in a meadow 450 m below a den. Some dens have only a single rookery while others are known to have as many as eight, all of which may be located in a compact area or spread out over several ha. Some of the same rocks used in the spring for basking also serve as rookeries, but some of the spring basking rocks become too shaded when the trees are fully leafed. A slab located on a flat or level ledge top is more likely to be used as a rookery than as a spring basking rock.

Gestating females were found at an additional 111 sites that were not checked at birthing time. All rookeries shared certain characteristics. All were exposed to the sun for at least part of the day. They provided shelter from predators, rain, and sun. Horizontal rock slabs from 10-20 cm thick with 34 cm clearance were especially favored. Thinner rocks probably became too hot. During clear weather snakes usually basked in the morning and sometimes again late in the afternoon.

After parturition, females spent considerably less time basking than before. When an aggregation of neonates was found, it was usually possible to find a postpartum female by looking under the birthing rock. The female was usually within 1 m of the young (215/278 litters).

Timing of Parturition

Birthing is known to have occurred from early August to early October (Table 3). Duration of birthing during a particular year averaged about a month (3-6 weeks). The duration was longest during wet summers because the snakes at high elevations were more adversely affected by the curtailment of their basking time. Thus although gestation was lengthened everywhere, it was lengthened less at lower elevations where the cloud cover was less. During seasons with much sun, snakes at high elevations compensate for the lower temperatures by thermoregulating. Cloud cover reduces the amount of time which they can thermoregulate effectively. Postpartum females were found with premolt litters as early as 9 August 1986 and as late as 16 October 1989. The latest date that a female was found in parturition was on 3 October 1989. The median date for finding postpartum females with litters (all records combined) was 5 September (Fig. 5). However, the mean for all years combined is 9 September (Table 3). Duration of the birthing period ranged from three to over five weeks in different years. The duration of parturition at a particular site was usually no more than a week. At one rookery rock, three of 11 females had completed parturition on 8 September 1989, and on 16 October, one female was found with a premolt litter probably about two weeks old. Thus duration of parturition at that site was three to four weeks during that particular year.

S. H. Harwig (pers. comm.) supplied data on 504 neonates from approximately 85 litters found in Pennsylvania from 1948 to 1979. The median date on which they were found was 15 September (22 August to 7 October). This suggests

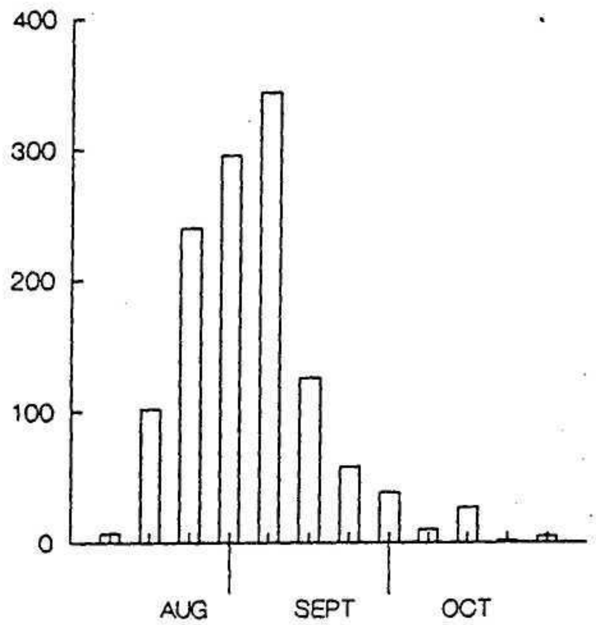

Fig. 5. Number (n = 1257) of neonatal *Crotalus horridus* seen. Neonates seen at the dens unaccompanied by post-partum female are included in Fig. 2 and not here.

Table 3. Birthing dates for *Crotalus horridus.* n= number of litters encountered in the field. The median date (mo/day) and the range of dates on which I found litters in the field is shown and the median and range of dates for birthing is estimated for the study region. Neonates encountered hibernacula unaccompanied by a postpartum female, are not included. A dash indicates that there was insufficient data from which to make an estimate. Number of days of rain and temperature deviation from normal for 1973-1990 in degrees C for April-August are listed for Luray, Virginia.

Yr	n	Field litters median (range)	Estimated parturition date median (range)	Days rain	Tdev. April-Aug
73	6	9/8 (9/2-11)	9/4 (8/21-)	60	-0.3
74	6	09/15 (8/27-9/27)	9/9 (8/24-9/25)	67	-0.6
75	2	9/12 (9/4-20)	9/10 -	59	-0.2
76	3	9/10 (9/6-13)	9/2 -	40	-0.3
77	35	8/23 (8/18-26)	8/18(8/4-31)	45	+0.8
78	10	9/7 (9/5-9)	9/5 -	49	-0.1
79	9	9/11 (8/25-9/18)	9/10 -	59	-0.6
80	2	9/20 (9/12-29)	9/2 -	44	-0.3
81	30	9/18 (8/15-9/26)	9/10 (8/14-9/23)	63	-0.6
82	28	9/9 (8/24-10/2)	9/5 (8/21-9/20)	59	-0.7
83	6	9/14 (9/5-10/3)	9/4 -	50	-0.2
84	18	9/13 (8/28-10/14)	9/9 (8/24-9/22)	54	+0.2
85	7	9/3 (8/16-9/10)	8/27 (8/14-9/7)	50	+0.5
86	31	8/29 (8/9-9/7)	8/20 (8/7-9/1)	45	+0.6
87	51	8/30 (8/19-9/11)	8/23 (8/10-9/4)	44	+0.8
88	18	9/4 (8/17-9/14)	8/30 (8/15-9/10)	46	+1.1
89	15	9/25 (9/4-10/16)	9/17 (9/1-10/3)	68	-0.6
90	7	9/8 (8/31-9/28)	9/3 (8/24-9/18)	61	0
$x \pm SD$(range)		9/9 ± 8.4 (8/28-9/22)	9/2 ± 9.2 (8/17-9/15)	54(40-68)	
sample range		(8/9-10/16)	(8/4-10/3)		

the median date of parturition was about 10 September, averaging approximately a week later than in my study area. During at least one year, 1989, pregnant females at a high elevation den on the Allegheny Front in Grant County, West Virginia, apparently entered hibernation before giving birth. Follow-up visits revealed no juveniles of that cohort.

Effect of Elevation on Timing of Parturition

For birthing sites of comparable exposure and aspect, each 300 m increase in elevation delayed the date of parturition by about 10-15 days on average. During summers with hot, dry weather, the delay was the least but when the summer temperatures were below normal and cloud cover above normal, the delay was somewhat more. Apparently during dear weather, the snakes can compensate for the lowered temperatures at higher elevations. The adiabatic lapse rate is 0.6° C for each 100 m. The difference in mean temperatures between Luray at 305 m and Big Meadows at 914 m is 2.9° C for July or 80% of the lapse rate. The rate is 210 m per 1° C. Before comparing birthing dates at different elevations, it is necessary to first eliminate confounding influences such as differences in aspects or amount of canopy cover. When we examine timing of parturition at sites of similar exposure but different elevations, the effect of temperatures is readily apparent. On 18 August 1977 at three well exposed south-southwest sites at elevations of 430-518 m, I found molts of neonates and postmolt neonates probably born on 4-8 August. At a similarly well exposed south slope at elevations of 915-1000 m, I found 2 litters and 3 pregnant females on 23 August. I estimated 18 days difference for 550 m and an average temperature difference of 2.6° C. In 1989, a very cloudy summer, I saw first litters on 4 September at an east-southeast exposure of 275 m. On 3 October, I found litters at an east-southeast exposure of 810 m. All young were estimated to be less than a week old. I estimate about 25 days difference in average dates between these high and the low sites. Difference in elevation for those sites of comparable aspects was 533 m (2.5 C). During the hot year, 1° C was equivalent to 6.9 days and during the cloudy year, 1° C was the equivalent of 10 days.

Seasonal Movements of Postpartum Females

After parturition, females spend considerably less time basking than during gestation. When an aggregation of neonates was found, the female was sometimes lying out with them, but more often she was under the birthing rock within 1 m of the young. Postpartum females usually stayed with their litters at the birthing rookery for seven to 10 days and then left, usually to forage, but in the case of some late birthings, towards hibernacula. Of 216 litters in which molting had apparently not commenced, 89.4% (194) were accompanied by a postpartum female, but only 40% (21 of 52) of litters that had started molting were accompanied by a postpartum female. Knowing the normal interval between birth and molting (8-16 days) it is possible to estimate the average length of time that the females remained with the young. With low temperatures of late September and October some postpartum females stayed two to three weeks with the neonates. On the average, females birthing in early September had about two weeks of intermittently favorable weather for foraging before arriving at the dens. Postpartum females found on 18 September 1979 and 2 October 1982 contained food items. David Storment (pers. comm.) reported that a captive Illinois female that birthed I on 26 August accepted food three and seven days later.

Females that gave birth in mid-September or later, probably did not usually obtain a meal before hibernating. Females that produced young the previous fall were rarely seen in the spring. Because of a fast lasting 3-12 and occasionally 21 months, they are emaciated and very hungry. One found on 19 May (1989) appeared near death, apparently from starvation. It is imperative that they take every opportunity to feed. During the active season following the year of parturition, the entire active season, except for one and sometimes two pre-molt episodes, is mostly spent in wooded areas. Only rarely will they have gained enough weight by mid-July to initiate vitellogenesis. By recapture, I recorded 40 instances of two or more parturitions and only three of these were at two year intervals with the balance at three to five year intervals.

Activity and Movements of Neonates

Neonates are gregarious and were often seen basking in physical contact with one another at the birthing rookery. They are wary and as soon as one makes a quick movement, they all usually quickly disappear under the rocks. Neonates usually stayed aggregated at the site of birthing for eight to 16 days until the initial molt was completed. Judging by follow-up visits, neonates born in August when temperatures were still high usually molted in eight to 10 days. Several liters born at one rookery in August all molted before their ninth day. Another litter bom in late August had not all molted after 12 days. Those born around early September (the median date) molted in 10-14 days. Two litters born in early September had not molted at eight and 12 days of age, respectively. Some stayed at the birthing rookeries for up to four weeks when temperatures were considerably below average. Two Utters had only partly completed molting after 32 and 39 days. On 15 October 1989, young from litters born between 28 September and 3 October were starting to molt but some born during the same time period had still not molted on 26 October when three premolt neonates were found at a birthing rookery, and a premolt and a postmolt young, probably all from the same litter, were seen at nearby hibernacula. When molting is delayed by cool weather, some neonates go to the dens before molting, but they tend not to enter hibernation until they have shed the proto-integument, and may continue basking for several weeks after the balance of the population has entered hibernation. Nevertheless, some are forced to enter hibernation before molting. In 1989, premolt neonates were seen basking at dens and birthing rookeries through 26 October and some of these probably had to enter hibernation without molting.

Neonates born around the average time (early September) will usually have about two weeks to forage before entering hibernation. Many of them do get food, usually young mice. Most of the neonates in my sample were premolt and in a gations at the place of birth. Many of those that were postmolt had apparently molted within a day and were still aggregated with their siblings. They are not often encountered once they have dispersed into the adjacent wooded areas to forage. Individuals found at dens on 27 September 1980 and 5 October 1986 contained large food items. One of two snakes seen at a birthing rookery on 29 September 1987 had fed. Of 11 neonates found dispersed in wooded areas near dens or birthing rookeries, three contained food (two on 11 September 1987, and one on 13 October 1973). Another of these 11 snakes, found on 9 October 1986, was 38 cm TL and had certainly obtained food in order to reach that length (neonates average 28 cm TL at birth). One recently molted neonate taken on 2 October accepted a young mouse a few days later. S. H. Harwig (pers. comm.) reported that a Pennsylvania neonate taken on 23 September disgorged a half-grown mouse on 25 September. Judging from the size and appearance of young-of-the-year seen at hibernacula during fall and spring, I believe that roughly half of them obtain a meal before hibernation. I do not believe that failure to find food during the first autumn is a serious mortality factor, except in the case of young born in early to mid-August, which because of warm temperatures and longer active time, would be subject to greater loss of yolk reserves. Twenty-five neonates born to Illinois females in late August were hibernated under simulated natural conditions (D. Storment, pers. comm.). Snakes were in hibernation from early October until April. Of 19 non-feeders, four died, but of the five that fed before hibernation, only one died. The low survival rate in nature, estimated at 39% for their first year and 60% over-winter (Martin, unpubl. data) is believed to be due mainly to failure to find adequate hibernacula and to predation. Starvation probably is a major problem for those individuals who still have not obtained a meal by June. I have found one-year-old snakes as late as 3 September that still had not molted for the second time and were no bigger (35 cm) than large neonates. One large meal, taken in June, will probably sustain a snake for a year, but growth rates are diminished.

Sufficiently low temperatures will induce neonates to leave the birthing rookeries before they molt and move towards dens. Once, on 28 September after two frosts had occurred, I found a loose aggregation of 16 snakes (some coiled, some moving) that included four premolt neonates and two postpartum females, spread out over a 150 m stretch of ridge top between a birthing rookery and an overwintering den. Some snakes were also seen at the birthing rookery (including two neonates) and at the den.

Fall Migration

Fall migration apparently begins in late August to mid-September, following the passage of cold fronts. Migrating snakes remain mainly in wooded areas, where the possibility of encountering prey may be better. I have found them coiled in an ambush position as in wooded areas near dens as late as 9 October. It is difficult to get precise data on the timing of this activity phase because some snakes of any age and sex can be found in the vicinity of dens at any time. However, around certain dens, there exist some rocks, apparently on migration routes, that tend to be used by snakes migrating in or out and not usually by snakes spending the summer in the den area. At the low to mid-elevations in the study area it is rare to even find snakes approaching the den area until late September but at northerly locations and at the higher elevations in the Allegheny mountains this may happen three weeks earlier. Once on 3 September 1989 at 1100 m in northern West Virginia. I saw 29 rattlesnakes a year or more in age within 500 m of a den.

DISCUSSION

Hibernation

The timber rattlesnake is known to hibernate communally throughout the northerly portions of its range. Most dens are reported to face in a southerly or westerly direction ranging from east-southeast to due west (Ditmars, 1907, 1930, 1939; Gloyd, 1928, 1946; Morgan, 1939; Swanson, 1952; Harwig *in* Klauber, 1956; Kauffeld, 1957; Anderson, 1965; Keenlyne, 1972; Galligan and Dunson, 1979; Stechert, 1980; Vogt, 1981; Brown, 1982, this volume; Petersen and Fritsch, 1986). Apparently the milder winters in Virginia permit overwintering at dens of less than ideal exposure. The reasons for selecting the more southerly aspects are obvious. They are the warmest, permitting a longer active time and a shallower hibernating depth. The snakes, however, are opportunistic, using whatever overwintering locations enable their survival and northerly aspects sometimes suffice. Most dens reported by these authors were stated to be located in ledges or in some cases, talus and scree slopes, but Gloyd (1946) in Kansas and Minton (1972) in Indiana reported that they may sometimes use burrows of mammals such as the woodchuck. Little information is available on elevations of dens. Wood (1954) reported dens in Virginia (apparently in southwestern Virginia, south of my study area) from 1700-4500 feet (518-1372 m). A den studied by Brown (1982) in northeastern New York was only 229 m in elevation. Maximum elevation at that latitude is expected to be much lower than in Virginia. In Wisconsin at a latitude similar to northern New York, Keenlyne (1972) found dens up to about 400 m. In southern New Jersey they have been reported hibernating along streams or springs in bogs (Burger, 1934; Kauffeld, 1957; Reinert and Zappalorti, 1989). Neill (1948) reported that they hibernated communally in limestone caverns in the Savannah River swamp, near Augusta, Richmond County, Georgia. Allen and Neill (1950), apparently referring to northern Florida and southern Georgia, reported that they will over-winter in a cave or limestone fissure, fox burrow, stump hole, pine roots, chimney rubble, or sawmill site.

Little information is available on hibernating depth. Noble and Claussen (1936) excavated a den in southeastern New York where the frost line is about 50-75 cm (USDA, 1941). The snakes were said to be in small groups in various crevices about *12* m in depth. Galligan and Dunson (1979) reported that the frost line in central Pennsylvania is usually 80 cm but that during the winter of 1976-77 it reached 1.4 m. Frost penetration would probably be less on a south or southwest facing slope, but unfavorably aspected dens at that latitude would have to be quite deep in order to protect the snakes from the occasional unusually cold winter. Brazaitis (1979) inserted a thermometer about 75 cm into a hibernating crevice in a southern New York den. Temperatures fell to no lower than 2° C during the coldest part of the winter.

Brown (1982) monitored overwintering body temperatures in three adults in a northeastern New York den and found that body temperatures were 15-16° C when the snakes became quiescent in the hibernaculum in September. This is the same temperature range which I noted at the warmest soil layer (45 cm) during time of peak ingress in October. He also found that body temperatures dropped as low as 4.3° C. Unfortunately he did not get emergence temperatures because two transmitters malfunctioned. The third individual still had not emerged on 25 May and may have died in the den.

There does not appear to be a threshold air temperature that signals the snakes to begin the migration and then to come in to the dens. Rather there appears to be a combination of factors or "zeitgebers" involved that signal the snake: 1) to begin the migration from summer range towards the den, and 2) to leave the woods and come into the den. Weather varies so widely from year to year that no single weather event (first frost, for example) forecasts a future weather event (weather too cold for activity and for safety). The calendar is a better guide to future conditions several weeks ahead than is the present weather. Apparently there is a window existing from about 26-30 September, when the snakes are prepared for a signal (a cold front) to enter the dens. However, an early or late emergence may disrupt their timing. Parker and Brown (1982) found that *Masticophis taeniatus* returned to dens a fixed number of days after emergence. Viitanen (1967) believed endogenous factors were involved in the return to the dens of *Vipera bents.*

When sampling and weather data were pooled for all the years of the study, certain trends are noticeable that could not otherwise be detected: The mean date of first arrivals at the dens during the end of September (Table 2) corresponds with the time that temperatures become too low for foraging and it also corresponds with the mean date for the first observance of frost (unpubl. data) and is two weeks before the official first frost date (USDA, 1941) recorded about *12* m above ground. The mean temperature at this time also corresponds with the mean temperature at the time of the last snakes found in hibernating crevices in the spring. The mean air temperatures at the mean dates of general emergence and general ingress correspond very closely (Figs. 2, 3, 4 and Tables 1 and 2). When mean dates of ingress and emergence are compared with mean temperatures the correlations and trends are apparent.

The move from the surface to the hibernating chamber is largely determined by day-to-day weather. A reversal of the thermal gradient may be responsible. During the 10-14 days that normally elapse from the time of the first arrivals until general ingress, fewer snakes are seen than in the period at and immediately following spring emergence. Even when favorable conditions with partly cloudy mild weather occur, much of the population still has not arrived at the dens or is already underground. The exposed rocks where rattlesnakes often bask so conspicuously in the spring following emergence are rarely used on the return to the dens.

Few rattlesnakes were seen after mid-October. Although temperatures during the three to four weeks following a general entrance into hibernation, are similar to those experienced during the three to four weeks prior to general emergence, far fewer snakes are seen in the late fall period than in the early spring. Several factors may be involved: 1) the layers of soil near the surface are cooling rapidly and wannest layers may be around 45 cm deep; 2) on many days the warmth from the surface may reach the snakes too late in the day so that ascending snakes are met with descending cold (Viitanen, 1967); 3) the angle of the sun's azimuth in late October is comparable to that in late February; and 4) during clear weather with little wind when insolation by the sun is most effective, by the time the warmth has penetrated to the snakes and brought them near the surface, the surface may actually be too hot to permit basking so the snakes may remain just below the surface.

The seeming lack of correlation between high, mean, and low temperatures with emergence is because it is difficult to predict the temperature of the ground from the immediate weather conditions. It is only when the means of temperatures and emergence are examined that a pattern emerges. The partial reversal of the thermal gradient in March sets the stage for emergence. Apparently the body temperature of the snake must be somewhere in the range of *5-8° C* before movement takes place and the snake then follows the thermal gradient upward and emerges to bask (during periods of favorable weather). Jacob and Painter (1980) found that while *C. viridis* is capable of movement at 1° C, they do not respond to the thermal gradient until they reach a body temperature of 6° C. There may be quite a bit of moving up and down in the den crevices before any emergence occurs. I have never seen a rattlesnake out on the first warm day of the year even when highs reached 23-25° C. Viitanen (1967) noted a similar activity pattern for *V. bents*. The surface reaches its highest temperature about 1400 hr but the highest temperature at 30-40 cm is not reached until about midnight (Hanks and Rasmussen, 1976). On the first warm days, before the warm isotherm reaches the snakes, they are met with the descending cold of evening thus forcing them down towards the warmer layers (Viitanen, 1967). As April advances the wanner layer ascends towards the surface. Eventually the warm layer reaches them early enough in the day so that a few snakes come to the surface. Selection would not favor snakes that left the hibernacula too soon. Snow and temperatures considerably below freezing often occur during the early emergence phase that precedes general emergence. The warming of the upper portion of the den to near 10-11° C apparently provides the signal to emerge and abandon the den crevice. Snakes that emerged early (before late April) usually returned to the den crevices. Perhaps the snakes may have been stimulated to abandon the dens only after the snake's body temperature remained at around 10-11° C for a certain minimum period of time exceeding 24 hr. Selection should favor snakes that delay emergence until that time because the chances of a snake requiring deep shelters after that date is lessened. The shallow spring shelters that are used in the basking period immediately after emergence might not adequately protect snakes that moved to them too soon. With the surface layers of soil warmer than the deep layers there may also simply be little incentive to stay in the dens. Many dens may not be deep enough to ever become isothermal. Even a limestone cavern den studied by Sexton and Hunt (1980) in Missouri did not remain at base temperature. The base temperature ranges from 8 to 15° C from the northern edge of this snake's range to the southern edge in the Appalachians. Whether *C. horridus* responds to the same temperature thresholds throughout its range is not known. Macartney (1985) believed that *C. viridis* in British Columbia had much lower activity thresholds than did the same species in California, where it was studied by Fitch (1949).

Galligan and Dunson (1979) compared deep (91.4 cm) soil temperatures from a nearby agronomy station, with emergence of C. *horridus* in Pennsylvania over a three year period from 1975-1977. They noted no correlation between emergence and air and ground temperatures but they found only five specimens (due apparently to a very low population) in the three emergence periods combined. However, I find that ground temperatures reported are very revealing when compared with my emergence data during those years (Table 1). Spring was exceptionally late in 1975 and exceptionally early in 1976 and 1977.

The three-day lag in time between peak emergence of adults and juveniles is apparently not due to different temperature thresholds. The fact that some juveniles emerged with the earliest emerging adults leads one to predict a different cause. The depth of hibernation may be the major reason for the difference in peak emergence times. Viitanen (1967) found differences in emergence time of *Vipera berus of* the same sex and age class, attributable to hibernation depth, but he also believed that adults emerged earlier to enhance reproduction. Drda (1968) found that juvenile *Agkistrodon contortrix* were deeper in a cave hibernaculum than were the adults. Resting snakes like to wedge themselves into tightly fitting crevices and my own observations indicate that small snakes favor tighter crevices than do large snakes. Crevices with narrow openings will only allow ingress of smaller snakes and indeed sometimes one sees different size snakes using different crevices within the same general area. Even at some dens where all snakes are using the same crevice or same crevices for ingress, the large crevices may have other side crevices opening up underground, or the crevices may narrow toward greater depths. We may envision the snakes in the hibernaculum moving towards the warmer deeper layers of the den as the isotherms retreat downward. On the average, the larger snakes simply cannot get as deep as smaller ones. Viitanen (1967) and Aleksiuk (1970) predicted that hibernating snakes should follow the thermal gradient and work by Sexton and Hunt (1980) and Sexton and Marion (1981) has shown that snakes tend to follow the thermal gradient and the stopping of snakes at a certain depth is caused either by the temperatures dropping too low for movement to be possible, or by the inability of the snakes to get any deeper due to the narrowing of the crevices. Obviously there will be more deep crevices that can accommodate small snakes than large ones. Some small snakes of course have entered different crevices adjacent to those used by the adults and some of these may not be so deep.

Summer Activity

The activity peak which I noted in early June, may be comparable to the vernal migration in search of foraging territory by *C. viridis* in Wyoming (Duvall et al., 1985). They noted movements as much as 10 km from the den and as much as 1 km a day and attributed these migrations to the patchy distribution of prey. I think that such long distance migrations as 10 km are rare among *C. horridus* in the Appalachians, but they certainly should be capable of traveling one km in a day and probably do so on occasion. Neill (1948) thought that *C. horridus* in Richmond County, Georgia, converged in the late summer from as much as 32 km to an area of limestone caverns in a swamp. There has, however, been no confirmation that they normally travel such distances.

Reproduction

Ditmars (1907) stated that timber rattlesnakes mate in the spring while still congregated at the dens. He did not, however, provide any supporting observations. Many authors since then in the popular literature, nevertheless, have repeated this assertion without adding any supporting documentation. Only Anderson (1965) has reported a spring-time mating (27 April in Missouri). I have received numerous reports from my correspondents of late summer-early fall matings, centered on August, but for most of these the exact dates were not available. I have one additional report (Max Nickerson, pers. comm.) of a mating during May, in Stoddard County, Missouri. Keenlyne (1978) suggested that mating might start in late July-early August, shortly after the onset of vitellogenesis when estrogen levels are high. He also suggested that mating might occur at any time until ovulation. A spring mating season is a logical assumption for a communally hibernating snake because the sexes are congregated and no time need be wasted searching for mates. I suggest that late summer mating is a vestige from a period of time during the evolutionary history of the snake when communal denning may not have been common. Mating over a 2-mo period, during the earlier stages of vitellogenesis and storing the sperm until ovulation may actually have an evolutionary advantage over restricting mating to a short period just before ovulation. The available evidence (Table 4) strongly indicates that late summer is the major mating season throughout the range of this rattle-snake. If the timing of mating is related to the physiological stage of the female's reproductive system, then the time of mating should vary slightly geographically. We should expect that northern populations, because of a longer hibernation, would have to initiate vitellogenesis earlier in the season in order to yolk the ova to full size by ovulation time in late May and early June. We might predict a geographic dine in mating dates ranging from mid-July to early September in the North to late August to mid-October or even later in the extreme South. The strong late summer-early autumn activity noted for this species is probably related to mating with adult males searching for female scent trails. Andren (1982) noted that male *Vipera berus* make long movements during the mating season of up to one km per day.

Whether male breeding cyclicity is completely endogenous, is influenced by temperature, or by female pheromones not known. Most likely, with both males and females, endogenous arcadian rhythms are influenced by photoperiod and by temperatures. Female pheromones may play a part in synchronizing the breeding cycle, not only among females, but possibly also with males.

Pregnant female rattlesnakes in this study usually used certain favorably exposed rocks for gestating and parturition. Jackley *(in* Klauber, 1956) reported that gravid female C. *viridis* in South Dakota used certain locations for birthing (often an abandoned prairie dog burrow), that he referred to as "rookeries." Kauffeld (1957) reported finding an aggregation of pregnant female *C. horridus* in New York during June, and speculated that they might spend the entire summer on the exposed ledges near the den. Keenlyne (1972) believed that these gestating and birthing rookeries, which in Wisconsin were usually slabs of rock located on grassy southerly slopes, were critical to the survival of this rattlesnake in the North. Harwig (1966) reported finding 17 females at one rock in Pennsylvania. Brown et al. (1982) and Reinert (1984a, b) found that females, especially gravid females, of this species used warmer and sunnier micro-habitats than did males in New York and Pennsylvania respectively. Reinert and Zappalorti (1988) found that in the Pine Barrens of New Jersey, with the absence of rocks, gestating female rattlesnakes used the edges of sand roads, sometimes located more than a km from the hibernating areas in the cedar swamps. The aggregating of gestating female viperids at certain spots in warm and sunny microhabitats, in the temperate regions of North America and Europe has been reported by (Finneran, 1953; Fitch, 1960; Viitanen, 1967; Diller and Wallace, 1985; Duvall et al., 1985; Gannon and Secoy, 1985; Macartney and Gregory, 1985).

Ditmars (1907) reported that near-term pregnant female timber rattlesnakes in the Northeast (New York, New England, and northeastern Pennsylvania) often returned to the dens for parturition. Macartney and Gregory (1988) reported that *C. viridis* in British Columbia usually returned to the den for parturition. I found that rattlesnakes in my study areas did not usually return to the dens for parturition except in the case of birthing rookeries located at the dens. In some instances, the only suitable place for gestating, was at the den. With the exception of a late-birthing female found with a litter near the den, 200 m from the rookery, on 16 October 1989 I believe that the instances in which I recorded parturition at the den, the females had spent most of the gestation period there. Another postpartum female was in a hibernating crevice on 22 August 1977 with a litter. I believe she moved there because the regular rookery got too hot. In the more northerly areas with colder winters perhaps selection has favored the habit of birthing at the dens. Additionally, the normal parturition time in the North overlaps the normal time of arrival at the dens. With the exception of 1974 and 1989 this was not the case in my study areas.

Neonates usually stay aggregated at the place of birth for 8-16 days. They usually begin dispersing towards foraging areas or hibernacula as soon as they molt, but some leave before molting although not before their eyes clear, just prior to molting. Advantages of aggregating may include

Table 4. Records of mating for *Crotalus horridus.*

Date	Locality	Source
21 Aug 1975	Shenandoah Nat. Park. Virginia	This study
13 Sept 1976	Shenandoah Nat. Park. Virginia	------
5 Sept 1978	Shenandoah Nat. Park. Virginia	------
27 July 1942	Westmoreland Co. Pennsylvania	S.H. Harwig (pers comm)
8 Aug 1954	Indiana Co. Pennsylvania	------
14 Aug 1965	Clearfield Co. Pennsylvania	------
8 Aug 1982	Jackson Co. Alabama	Kevin Dodd (pers comm)
2 Aug 1933	New Jersey-	Hook, (1936)
27 April	Jackson Co, Missouri	Anderson (1965)
3 Sept	Chesapeake Co., Virginia (capt)	Martin and Wood (1955)
5 Aug 1987	Jackson Co. Illinois (capt)	David Storment (pers comm)
9 Aug 1989	Jackson Co. Illinois (capt)	------
15 Sept 1978	Passaic Co. New Jersey	Randy Stechert (pers comm)

defense, conservation of moisture and heat, and imprinting on the place of birth. Graves (1983) found that when neonate *C. viridis* are disturbed, they give off a scent that acts as an alarm. A rapid move on the part of one may also have a ripple effect on the balance of them. Duvall et al. (1985) found that subcutaneous water loss decreases after the proto-integument is shed. I have noted that premolt neonates seem to be reluctant to enter hibernation and will continue basking past the normal time for ingress, apparently in an effort to shed the skin.

I found that postpartum female timber rattlesnakes usually stayed with the neonates seven to 10 days. Although there are scattered references to females having been found with litters (Table 5), in most cases, the snakes were either collected or no follow-up observations were made to determine how long the mothers stayed with their young. Duvall et al. (1985) stated that postpartum female *C. viridis* in Wyoming stayed with their young for several days. Graves (1988) noted that undisturbed postpartum females in that population stayed with their young as much as 16 days. Macartney and Gregory (1988) found that postpartum females entered hibernation one to 10 days after birth. Parturition during their study, however, was apparently delayed past the normal time by the weather and occurred at or even past the normal time for ingress. Wharton (1966) reported what he regarded as "guarding" behavior of the mothers towards the neonates in the cottonmouth, *Agkistrodon piscivorus conanti.*

Crotalus horridus and possibly some other rattlesnakes, may have evolved a recuperative period that corresponds roughly with the time that the neonates are aggregated. The mere presence of a large rattlesnake might discourage some mammalian predators that otherwise would not hesitate to take a neonate. Parental care has not been reported for nonvenomous live-bearing snakes and would be of little defense against a predator. It might seem that the postpartum female rattlesnake, who has not fed for a three and perhaps 12 month period would best serve herself by leaving immediately after parturition, in search of a meal in order to replenish her badly depleted fat reserves. However, the selective advantage may lie with delaying the search for food until the litters start to break up and disperse. Although it is possible that the postpartum female is responding to the grouped neonates, I think that is not the case because follow-up visits usually indicated that the mother began moving away from the rookery, before the young did. On the other hand, she may be responding to a decrease or change in odor after the eyes of the neonates clear just prior to molting. The propensity for postpartum female rattlesnakes to stay a week or more with the neonates may be found to be more widespread than the literature now indicates.

Brown and Maclean (1983) and Graves et al. (1986) found that postmolt young-of-the-year *C. horridus* and *C. viridis,* respectively, were able to follow scent trails of conspecific adults in the laboratory. Reinert and Zappalorti (1988) found evidence that young-of-the-year C. *horridus* in the Pine Barrens of New Jersey were apparently following adults, including males, in some cases for distances in excess of 1 km, to the denning areas. Young snakes may learn, not only the location of the overwintering dens, by following the scent trails of the adults, but also the locations of ancestral trails leading to summer feeding grounds.

Geographic Variations in Phenology

Although there have been no papers on the phenology of C. *horridus,* some phenological data can be gleaned from the available literature (Table 5). In the extreme northeastern part of the range, in northeastern New York, Brown (1982, this volume) found ingress occurring through most of the month of September but peaking during the last half of the month. Gloyd (1928) reported ingress as late September to mid-October in eastern Kansas. Brown (1982, this volume) reported that first emergence occurs around 20 April in northeast New York, with general emergence in mid-May and with the last snakes leaving the dens in late May (the earliest snake was 8 April with emergence peaking on 13 May). A little further south, first emergence is reported to be about 15 April in Connecticut (Petersen and Fritsch, 1986). Trembley (1970) reports that emergence in northeastern Pennsylvania correlates with blooming of the apple trees.

Table 5. Phenological records for *Crotalus horridus*.

mo/day (yr)	Rattlesnakes at Overwintering Dens Locality	Source
5/7	New York	Ditmars, 1930
5/1, 5/15	New York	Kauffeld, 1957
4/28-5/27	Northeastern New York	Brown, 1982: Brown, this volume
4/27 (1941). 5/8	Venango Co., Pennsylvania	Swanson, 1952
4/23-4/30	Centre Co., Pennsylvania	Galligan and Dunson, 1979
4/22, 4/30 (1986)	Pine Barrens, New jersey	Reinert and Zappalorti, 1988
4/30 (1926)	Ottawa Co., Kansas	Gloyd, 1928
4/23 (1928)	———	
4/17-20	Western Missouri	Anderson, 1965
5/1 (1965)	Franklin Co., Kansas	Smith et al., 1983
4/25 (1966)	Jackson Co., Missouri	———
5/2 (1966)		
4/13 (1968)	Lafayette Co., Missouri	———
4/15 (1968)	Pettis Co., Missouri	———
4/16 (1977)	Pettis Co., Missouri	———
9/7-10/16	Northeastern New York	Brown, 1982; Brown, this volume
10/1	Marshall Co., Kansas	Ditmars. 1939
10/25, 10/26 (1985)	Pine Barrens, New Jersey	Reinert and Zappalorti, 1988
10/2 (1978)	McDowell Co., North Carolina	Martin (unpubl)
9/29 (1979)	Avery Co., North Carolina	———
	Females with Litters	
10/29 (1965)	Franklin Co., Kansas	Smith et al, 1983
9/12 (1967)	Pettis Co., Missouri	———
9/15 (1967)	Pettis Co., Missouri	———
7/25 (1977)	Pettis Co., Missouri	———
8/29 (1977)	Jackson Co., Missouri	———
8/21 (1934)	Venango Co., Pennsylvania	Swanson, 1952
8/22-10/7 (1948-1979)	Pennsylvania	S. H. Harwig (pers. comm.)
8/30 (1985)	Pine Barrens, New Jersey	Reinert and Zappalorti, 1988
8/28 (1978)	McDowell Co., North Carolina	Martin (unpubl.)
9/7 (1984)	Madison Co., North Carolina	———

Vogt (1979) stated that first emergence in Wisconsin is late April to early May with peak emergence correlating with blooming of the apple trees. Ditmars (1907) stated that most have left the den crevices by 15 May in southern New York. Reinert and Zappalorti (1988) in the Pine Barrens of southern New Jersey, found emergence to occur in late April to late May and ingress from early October to early November. Wood (1956) reported earliest emergence in Virginia at 16 April. Anderson (1965) thought emergence was usually about 17-20 April in western Missouri. Gloyd (1928) found them at dens in late April in eastern Kansas and said that they had usually all left the dens by mid-May. Burt (1933) reported them active as early as 3 March in Kansas. Wright (1986) reported a western Virginia adult found still on summer range 26 September, eating what appeared to be a chipmunk. Fitch (1958) reported the latest activity at 26 October in Kansas. Hamilton and Pollack (1955) stated that in west-central Georgia, they are occasionally found on the surface anytime in the winter when the weather is suitable. On the other hand, 100 km further north in South Carolina, Gibbons (1972, 1977) found them active from late April-October and occasionally November and stated they are not often found before May. Differences in methods probably account for this seeming discrepancy. Hamilton and Pollack's (1955) snakes were collected by troops on maneuvers who were likely to encounter snakes basking at their over-wintering sites, whereas Gibbon's snakes were mostly found crossing roads. Walker (1963) reported them most common from October-December in southern Louisiana.

Emergence time in northeastern New York (Brown, 1982, this volume) is comparable to that at the higher elevations of 900-1100 m in Virginia and West Virginia. Ingress on the other hand is earlier in New York and apparently occurs at higher temperatures. Rattlesnakes in southern New Jersey usually over-winter in wet boggy places near the headwaters of streams (Burger, 1934, Kauffeld, 1957, Reinert and Zappalorti, 1988), where both emergence and ingress are retarded by the temperature lag.

Phenological observations are available for the timber rattlesnake in Missouri and Kansas (Anderson, 1965; Gloyd, 1928; Smith et al., 1983) at roughly the same latitude as northwestern Virginia. Elevations there, averaging about 300 m, are comparable only to the lowest sites in Virginia, however. Ingress in those western areas appears to be a little earlier than at similar elevations in Virginia but roughly comparable to ingress at middle elevations in Virginia, 500-800 m. Spring emergence is perhaps a few days earlier in the western part of the range, even at a comparable elevation. Weather systems move from west to east at that latitude bringing both fall and spring a little earlier in the West. Because of the continental location, winters are slightly colder, so selection should favor a slightly earlier ingress. Furman Coggins (pers. comm.) of Jackson County, North Carolina reported that in the high mountains of southwestern North Carolina with elevations of 750-1500 m, first emergence is usually late March-early April, with peak emergence in late April-early May. He has however, on rare occasions, seen rattlesnakes at the dens during every month of the year and has seen them on the roads as early as late March. Milder winters permit occasional basking. With a shallower frost line, one would expect overwintering dens to be at a shallower depth on average than in areas further north. One can predict that south of the 8° C January isotherm, a line that runs across southeastern North Carolina and through the Gulf states to northeastern Texas, most dens should be shallow individual shelters and sporadic basking should occur at anytime there is favorable weather in the winter. The observations by Hamilton and Pollack (1955) in Georgia, and (Walker, 1963) in Louisiana, lend support to this hypothesis. Allen and Neill (1950) however, apparently referring to Richmond County located in the Fall Line section of Georgia, report 81 rattlesnakes taken from a den. They did not provide details.

Some aspects of the phenology of C. *horridus* are quite similar to that reported for other North temperate zone viperids such as *C. viridis* in western North America, (Diller and Wallace, 1985; Duvall et al, 1985; Gannon and Secoy, 1985; Macartney, 1985;) *Agkistrodon contortrix,* in eastern North America (Fitch, 1960); and *Vipera bents* (Saint Girons, 1952, 1981; Duguy, 1963; Naulleau, 1966; Viitanen, 1967; Prestt. 1971; Phelps, 1978; Nilson, 1980; Andren, 1982) in Europe. For all of these, first emergence is usually in late March or April, a general emergence in late April or May, followed by spring migration. Ovulation occurs late May-June. Birthing occurs from early August to early October. The fall ingress may begin as early as late August and ends as late as early November. Jacob and Painter (1980) studied C. *viridis,* in New Mexico where basking at the dens during favorable weather in November and December occurred. Milder fall and winter weather at that latitude allows surface activity that is rarely noted further north.

Successful reproduction is a major requirement for a, species throughout its range. The climate must permit completion of gestation. At the climatic fringes of a species range, one might predict occasional failures. Variation in year-to-year timing of emergence is important because of its effect on timing of parturition. Gestation is timed so that it is centered on the warmest time of the year. This means ovulation should occur in late May or early June when emergence occurs at the normal time, but with emergence coming early or late, ovulation is shifted accordingly. Fitch (1949) noted 5 week variation in timing of emergence from yr to yr among *C. viridis* in Madera County, California. I noted peak emergence varying 26 days annually, from 18 April to 14 May (Table 2). We can predict that the timing of emergence would vary more in climates with mild winters because most snakes would over-winter in shallow shelters where they are more easily roused by a few days of unseasonably warm weather. Jackley *(in* Klauber, 1956) reported that in South Dakota, *C. viridis* only left the dens about a week earlier than normal, during a year in which first snakes were on the surface in late March, due to spring coming a month early. Apparently the deep dens there were slow to warm up in spite of warm air temperatures.

Apparently ovulation among all North temperate zone snakes occurs at about the same time (late May-June). This allows gestation to occur at the time when temperatures are most advantageous for gestation (Gregory, 1977). Saint Girons (1982) noted that the date of ovulation in vipers remained fairly constant in all temperate geographic areas. Of course some year-to-year variation should be expected because of variation in emergence dates. Climate limits the distribution of this and other temperate region snakes, primarily by the constraints that it places on reproduction. The active season must be of sufficient length and warmth so that gestation can be completed on average, 10-14 days before hibernation. At the climatic extremes we should predict that, due to occasional years of subnormal temperatures and above normal cloud cover, the pregnant females must sometimes carry the unborn young into hibernation. The consequences to the mother and young are unknown but could probably be determined experimentally in the lab.

Although parturition in temperate zone snakes always occurs in late summer or fall, fairly wide .year-to-year variation has been reported ranging in the different populations from as early as late July to as late as October. The gestation period of the timber rattlesnake, as is that of most temperate zone snakes, is centered on the wannest time of the year, June-August. Shine (1977) pointed out the importance of synchronizing the reproductive cycle in temperate zone snakes, so that gestation occurs when temperatures are favorable.

Blanchard and Blanchard (1940) showed that the length of the gestation period is affected by temperature. They found that each degree C was equivalent to 8.1 days in its effect on the length of the gestation period in *Thamnophis sirtalis.* This is within the range that I found (1 degree C was 74 equivalent to 6.9-10 days). Fitch (1949, 1960); Viitanen (1967); Gregory (1977); Macartney (1985); Saint Girons (1982) and Charland (1989) have all noted delays in parturition among temperate zone snakes caused by late emergence or below normal temperatures and above normal cloud cover. This becomes a critical factor only where a species' climatic limits are approached due to latitude or elevation. Macartney (1985) found some births among *C. viridis* as late as 23 October in British Columbia, past the normal time of hibernation in that area which is early October. Macartney

(1989) reported that neonates of that species entered hibernation 1-7 days after molting and females entered hibernation 1-14 days after parturition. Charland (1989) noted that pregnant female *C. viridis* in an outdoor enclosure still had not given birth by 4 October when they were released. Viitanen (1967; reported that during several years in Finland, due to low temperatures, some pregnant female *Vipera berus* had to carry the unborn young into hibernation. He also found a neonate on 10 July apparently born in the spring.

A late summer-fall activity peak has often been reported for C. *horridus* (Neill, 1948; Liner, 1954; Walker, 1963; Minton, 1972; Gibbons, 1977, Dundee and Rossman, 1909). There are at least four reasons for the late summer-fall activity: 1) mating, 2) dispersal of neonates, 3) fall foraging, and 4) fall migration.

CONCLUSIONS

The timber rattlesnake has evolved behaviors that allow the various life history events to occur at the most advantageous times. Endogenous rhythms strongly influence the return to the overwintering dens—thus the calendar is the best guide to predicting fall ingress. Nevertheless, various vegetational indicators provide the best indicator for predicting spring emergence. Endogenous rhythms probably influence the timing of the onset of the reproductive cycle, but the duration of the cycle is strongly influenced by weather.

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